High and low Dimorphism.

With an account of certain Tanaidae of the Bay of Naples.

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I. Introduction.

The occurrence of high and low dimorphism has for long been known to collectors of insects, and the phenomenon is probably familiar to anyone who has seen a series of the males of the common Stag beetle or indeed of almost any beetle in which the sexes are distinguished by well-marked structural differences. It consists essentially in the existence among the males of any species of a graduated series, as regards size and the development of the secondary sexual characters, such that the smaller males have relatively poorly developed secondary sexual characters while the larger males attain to a much greater relative development of those characters. The smaller males are then termed "low", and the larger males "high": when there is a more or less abrupt transition in point of numbers from high to low males we may most properly speak of a high and low dimorphism existing in the males of that species, but we also apply the term more loosely to those cases in which no such abrupt transition is proved to occur.

The object of the following pages is to extend the application of this phenomenon to several new cases, to endeavour to trace it to its causal connection in the general manifestation of the living organism, and to indicate its bearing upon the problem of organic change. It has been found possible to trace the existence and influence of the principle which underlies this phenomenon in very

various and not closely related groups of animals, but it will be noticed that all my instances are drawn from the Arthropoda. I do not believe that this limitation has any real significance; it is simply owing to the fact that the Arthropoda in the possession of a rigid exoskeleton and in the habit of changing it as a whole in ecdysis, offer very favourable material for the observation and measurement of small differences in structure. I venture to suppose therefore that the rules which we are able to formulate for this class will be of general applicability.

At the outset a definition must be given of two broadly distinguished types of high and low dimorphism, which I have termed facultative and definitive respectively. In all the cases which have been hitherto observed the males on the assumption of the adult state cease to grow or to undergo exuviation; consequently the high and low forms which they have assumed are permanent and do not suffer any further change. This I call definitive high and low dimorphism. But there occur cases in which growth continues after the assumption of sexual maturity, and under these circumstances I have called the very remarkable kind of dimorphism which may result, facultative, because in these cases the low male becomes converted into the high.

To the category of facultative dimorphism we now turn.

2. Facultative high and low Dimorphism.

A. *Inachus scorpio.* For more than a year a great number of this crab, which is exceedingly common in the Bay of Naples, has come under my observation almost every week, so that I have been able to gain a fairly just idea of a sample of the whole population. The specimens are very commonly infected with a species of *Sacculina*, which was my particular object of study, but the following observations refer to uninfected males. In order to ascertain that I was really dealing with uninfected normal males, each crab after measurement was dissected and a thorough search was made for the internal stages of *Sacculina*. These were very frequently found in a great number of crabs which showed no external trace of the parasite, and these crabs were of course rejected from our computation of the normal specimens, since the presence of the parasite profoundly affects the structure of the crab as will be shown in a future work.

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The normal uninfected specimens of the male occur during the breeding season (February to August) under three chief forms which
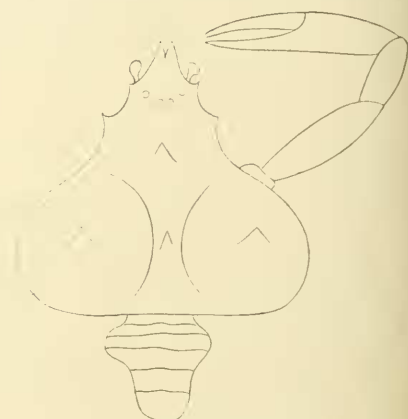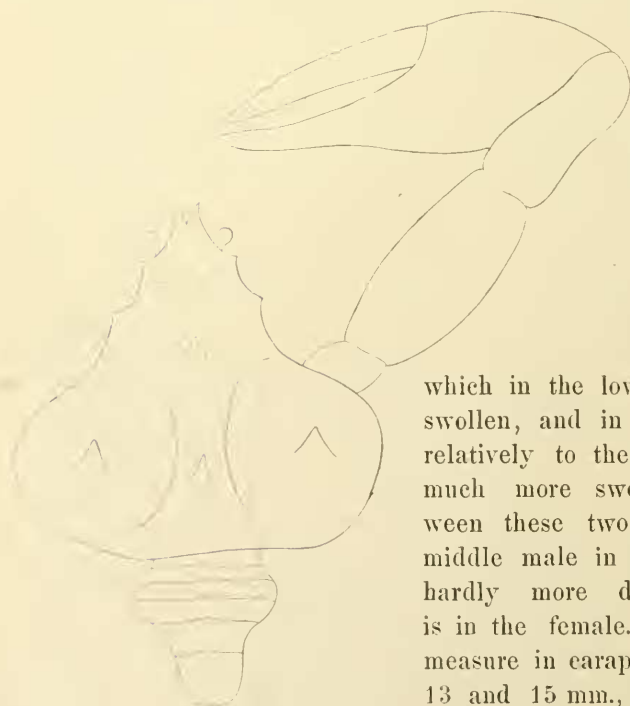

Fig. 1.

Fig. 2.

Fig. 3.

I term low, middle and high. These are drawn schematically in the Text Figures 1, 2 and 3 respectively. The secondary sexual character affected is the chela, which in the low males is slightly swollen, and in the high males is relatively to the size of the crab much more swollen, while between these two types comes the middle male in which the chela is hardly more developed than it is in the female. The low males measure in carapace length between 13 and 15 mm., the middle males 16—18 mm., and the high males 19—26 mm. During the breeding season the number of middle males is small, compared to the frequency of the other two types. We may express the relation

between the general size of the male and the degree of development
of the chela by the curve of average growth given in Diagram 1
which was made from measurements on 496 males taken at random
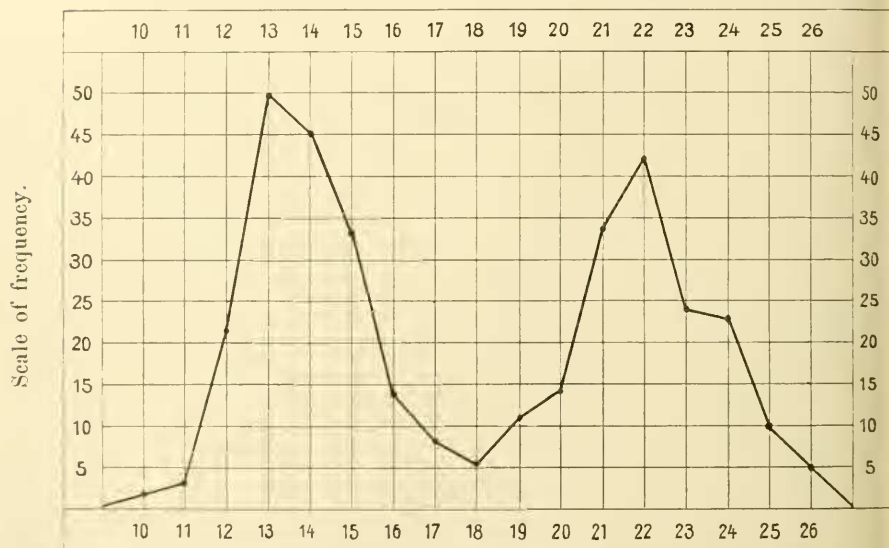during the breeding season.

Chela breadth in millimeters.
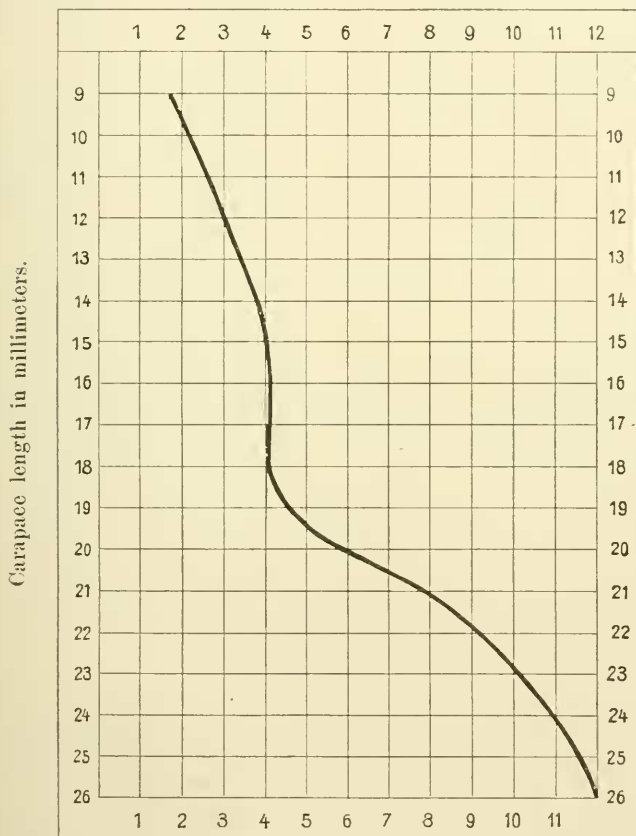
Textfigure 4 (Diagram 1).

The curve is constructed from Table 1 in Appendix 2 (see below
page 338) by drawing a line through the average chela breadth asso-
ciated with each particular carapace length, and the shape of the
curve expresses clearly the fact that in crabs between 15 and
19 mm. carapace length there is no average increase of breadth in
the chela, and that the increase in breadth is more rapid in crabs
after 19 mm. carapace length than between 9 and 15 mm. The same
thing applies to the average chela length, so that it is growth in the

whole chela that is arrested at the middle stage. Now among the middle males, there also occur a very small number of crabs measuring between 16 and 19 mm. in carapace length, which exhibit a swollen chela intermediate between the low and high males. The very low frequency with which such crabs occur is exhibited in the Frequency Curve Diagram 2.

Carapace length in millimeters.

Textfigure 5 (Diagram 2).

This curve shows the frequency with which males of all sizes with swollen chelae occur during the breeding season, the middle males with flat chelae being omitted. It is seen that there are two modal points of greatest frequency, one at 13 mm. carapace length, the other at 22, and these correspond to the low and high males respectively. Now if we dissect a large number of crabs with swollen chelae during the breeding season we find that in all cases the testes are very large and spermatogenesis is in full activity, but the testes of males with flat chelae are obviously reduced and sections show that spermatogenesis is in abeyance. The curve in Diagram 2 represents, therefore, a sample of the breeding males of the population under consideration, which are thus seen to be essentially differentiated into high and low forms. What then is the explanation of the middle males with flat chelae, which take no

active part in the breeding season? The explanation of their occurrence is given by examining the males that occur during the winter months, when reproduction is not going on. We find at that season a few high males, presumably left over from the passed summer, but instead of any low males we have an assemblage of crabs measuring from 5—19 mm. carapace length, all of which exhibit the flat type of chela and reduced testes. What happens is this: the low males before they can take part again in the breeding season have to pass through a period of active growth in which the sexual functions are suppressed, in order to attain to the condition of high

Fig. 6.

males. This period of growth and sexual suppression is generally passed through in the winter, but this is not necessarily the case, and so we have the phenomenon of the middle males with flat

Fig. 7.

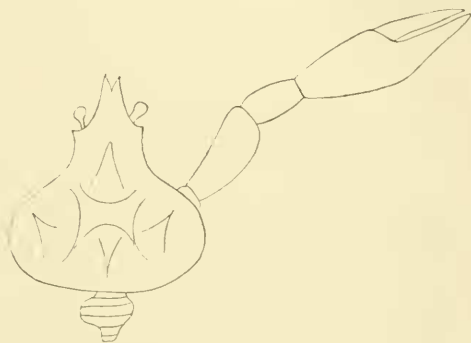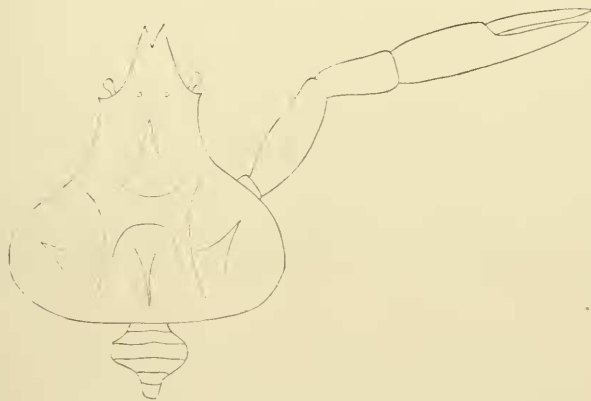chelae and nonfunctional testes occurring in the breeding season, while the breeding males are differentiated into high and low forms.

B. *Inachus thoracicus*. This species is closely allied to the foregoing, but is clearly differentiated in its greater relative length, in the larger size of the dorsal tubercles, and by the presence in the male of a large ventral shield. I have not been able to examine

a large series of males, but it appears that a similar phenomenon of dimorphism also occurs in this species. Figures of low, middle and high males are given in Textfigures 6, 7 and 8 respectively.
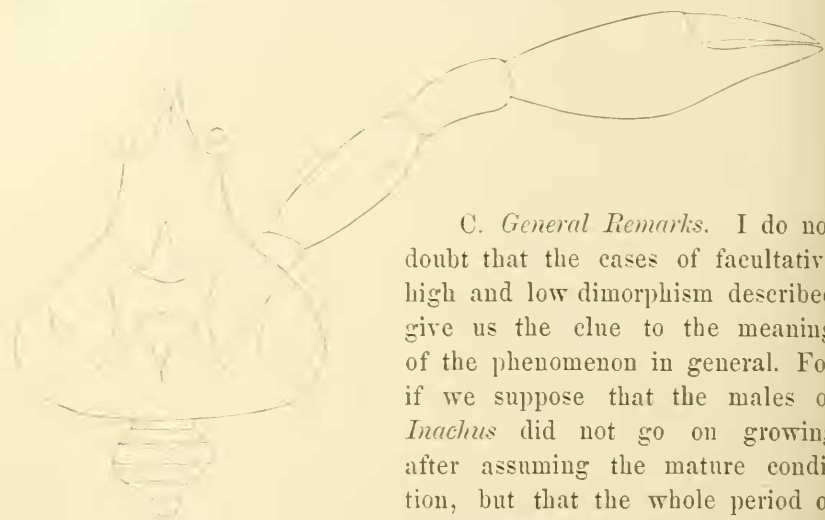

Fig. 8.

C. *General Remarks.* I do not doubt that the cases of facultative high and low dimorphism described give us the clue to the meaning of the phenomenon in general. For if we suppose that the males of *Inachus* did not go on growing after assuming the mature condition, but that the whole period of growth was relegated to a larval state, we should have a case of definitive high and low dimorphism in the males. As it is, however, we have the resumption in the middle males of a kind of larval immature condition which occurs after a temporary assumption of the sexual state in the low degree. This phenomenon points to an antagonism between growth and sexual maturity as the explanation of the occurrence of high and low dimorphism, an antagonism which is widely evidenced in organic nature. But to go further into this matter at present would be a digression from our main descriptive theme.

3. Definitive high and low dimorphism.

A. *Gnathia maxillaris.* In a small paper in this journal (6) I described some facts which appeared to show that there were two critical periods for the transformation of the larva into the adult male, firstly when the larva had reached about 2 mm. in length and again at about 5 mm. It will be remembered that the larva of *Gnathia* which undergoes metamorphosis into the adult is a swollen ectoparasite on fish known as Praniza, but another larval form occurs which I called the giant segmented larva, and this is most fre-

quently met with measuring about 4 mm. This latter larval form never metamorphoses into the adult, but probably attaches itself again to a fish and does not become adult until after passing again into the Praniza state. Although all the points contended for in my paper were by no means satisfactorily proved, the following facts are certain.

1. The adult male does not go on growing after attaining maturity.

2. Its range of size is immense, varying in the males from 1—8 mm.: this range of size being dependant on the amount of time spent in the larval life.

3. A large sample of males collected during full breeding-time fell into a distinctly bimodal curve in relation to size.

4. Corresponding to the two modal sizes, the males fell into two groups which showed somewhat different frequencies with respect to the measurement of an index describing the shape of the mandible, but owing to the difficulties of measurement I cannot lay much stress on this point.

5. At certain points in the larval history, but especially at the period of medium growth, i. e about 4 mm., a special retrogressive larva occurred which never passes to the mature condition from that state.

These facts appear to me sufficient to show that in this species in the Bay of Naples there is an antagonism between growth and maturity which tends to establish a division into high and low males.

B. *Leptochelia dubia*. (The reasons for assigning the limitations to this species are given in Appendix 1, pag. 333—335, and also the relation of the males I have found to those of FRITZ MÜLLER).

The males are distinguished from the females of this species by the greater size and different structure of the chela and of the first antennae. Males are figured in Plate 20, Figs. 1—2 and females in Figs. 11—13. The males up to the last ecdysis but one resemble the females; in the last ecdysis but one they assume the form shown in Fig. 10, and from this form they pass to the full adult condition which is permanent, the male ceasing to grow after this point.

The males differ greatly in size, from 2—4 mm. in length, and with this difference in size is associated a marked dimorphism, the larger males having immensely developed chelae (Fig. 7) while the

chela of the smaller males is quite disproportionately reduced
(Figs. 8 and 9). This is indicated in the following diagram 3, which
is constructed from Table 2, in Appendix 2.

Chela length in mm.
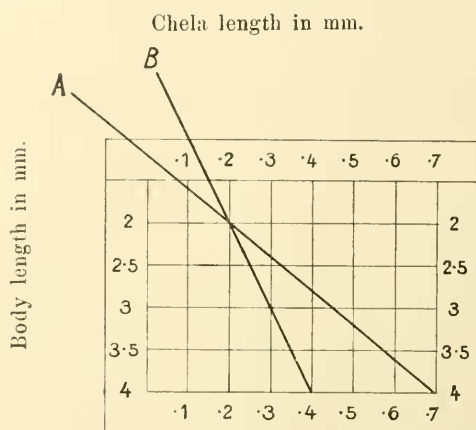
Textfigure 9 (Diagram 3).

It is here seen that the line of actual growth A of the chela rela-
tively to the body length, falls altogether outside the line of pro-
portionate growth B. I have been unable to determine whether
the high and low forms constitute a bimodal curve of frequency,
but this appears highly probable from the fact that several species
have been made out of them differing in the degree of development
of the chela.

C. *Orchestia Darwinii.* According to FRITZ MÜLLER (1) the males
of this species are sharply divided into two categories which differ
in respect to the form and degree of development of the chela. If
the males of both these forms were really adult members of the
same species we probably have here a case of high and low
dimorphism. DELLA VALLE however in his Monograph on the
Gammarini of the Bay of Naples throws doubt on MÜLLER's obser-
vation, but not with very sufficient reason.

D. *Forficula auricularia.* The classical case of high and low
dimorphism in the males of this species was described by BATESON &
BRINDLEY (2) from the Farne Islands. The 583 males, measured in
respect of the forceps, fell into a markedly bimodal curve, and
although measurements to show the correlation of this character with

the total length are not given, the authors state (Footnote p. 589): "There is nevertheless no doubt that the ratio of the length of the forceps to the total length is higher in high males than in low".

E. *Xylotrupes gideon* and the Lamellicornia. The dimorphism in *Xylotrupes gideon* has been described in BATESON & BRINDLEY's paper already referred to. The curve representing the relative frequency of high and low males was markedly bimodal.

In the whole order of Lamellicornia, wherever highly differentiated secondary sexual characters occur, the essential feature of high and low dimorphism can be seen, i. e. the association of highly developed secondary sexual characters with a large size and their reduction with a decrease in size among the males of the species that exhibit the phenomenon.

F. Pectinicornia. The character here chiefly affected is the mandible of the male. The essence of high and low dimorphism is here also apparent in all the species showing sexual differentiation. The curve, however, obtained by BATESON & BRINDLEY for a sample of *Lucanus cervus* was unimodal [1].

4. The correlation between the secondary sexual characters and the primary sexual character.

I am unable to enter very widely into this highly important aspect of the question without encroaching on a subject which forms the chief part of a work that I hope soon to publish. It is however well known from the facts of ordinary and parasitic castration, and of ovariotomy, and from observations on animals with abnormal genitalia that a close correlation exists between the primary and secondary sexual characters. I may also revert again to the facts described for *Inachus scorpio* (see page 316), where it was found that the middle males with flat female-like chelae always had reduced testes in which spermatogenesis was not active, as is also the case with low males in winter, when they too have flat chelae and small

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[1] Certain cases of high and low dimorphism have been suggested by GIARD (3) as due to the effects of parasitic castration. Although this may be the case in certain instances, it is hardly possible that a phenomenon of such wide distribution associated with particular stages in growth in totally different groups of animals can be always due to a parasitic affection. This is certainly not the case in the facultative dimorphism of *Inachus scorpio*, and it can hardly be doubted that we are dealing with essentially the same kind of fact there as in definitive dimorphism.

testes. This case is of particular interest to us because it proves that the form and development of the chela is correlated with the primary sexual development, and also that the phenomenon of high and low dimorphism is due to the assumption of particular states of sexual development at particular stages of growth.

I know of no observations upon the primary sexual development of high and low insects, but it can hardly be doubted that this class offers no exception to the universal rule that the secondary and primary sexual characters are here too closely correlated. But in the case of insects a special word of warning is needed. It has been proved in several cases (OUDEMANS 4 and KELLOGG 5) for butter-flies and moths that the destruction of the rudiment of the gonad in the larva has absolutely no effect on the development of the secondary sexual characters. This apparently contradictory result is only contradictory in appearance: because it is possible to prove, as I intend to show in another work, that the development of the secondary sexual characters in general is not due to the presence of a corresponding differentiated sexual gland, but that the differentiation of both the secondary and primary sexual characters is due to a third factor, which I will call the primary sexual development, and which may be uninfluenced by the destruction of the germinal cells at an early period.

It is confidently assumed here that the phenomenon of high and low dimorphism, both facultative and definitive, is due to a parti-cular kind of evolution of the primary sexual development in the growth of the individual, such that the males tend to become split up into high and low forms differing both structurally and physiolo-gically in their sexual nature.

5. Evidences of high and low dimorphism as a means of progressive differentiation.

The principle of high and low dimorphism has been shown to affect the males of various widely different species, and to constitute a differentiating factor within the limits of these species. We may now enquire whether this principle of differentiation may not extend outside the limits of a species and exert a controlling influence in the general evolution of organic groups. It appears that if this is the case we ought to be able to observe a certain relation between the male secondary sexual characters of the species which constitute

a group of this kind, a relation of such a character that on the whole the larger species should exhibit more highly differentiated sexual characters in proportion to their size than the smaller species. In other words in such a group of closely allied species, there should exist, besides high and low individuals within the limits of the species, also high and low species, if the principle of high and low dimorphism has exerted an influence on the evolution of the group. Now this is exactly what is found in no questionable manner in the groups which I have examined, in all of which the phenomenon of high and low dimorphism within the limits of the species is also apparent. These groups are the Tanaidae, Lamellicornia and Pectinicornia. We shall show that in these groups various series can be traced from species with larger males which exhibit the phenomenon of high and low dimorphism, to smaller and smaller species in which the secondary sexual characters of the males become more and more reduced, so that these smaller species are to the larger what low males are to the high males within the limits of a single species. It is not our purpose to maintain that this factor has been the essential factor in the process of specific differentiation, because in this process there are two possibly separate factors, firstly the factor of structural modification and secondly the factor of sexual incompatibility which prevents fertile intercrossing, but we can maintain with certainty that the principle of high and low dimorphism has played an important part in the structural modification of the group. The argument followed is one of phylogenetic reconstruction, and this is always hypothetical, but our advantage is this that it is indifferent to us which way the series leads whether from high to low or low to high, and indeed it does not matter whether the actual series we trace is a true one; all we require is a certain quantitative ratio between the size of the male and the degree of development of the sexual characters of the various closely related species in a group, and when this is proved our point is proved also. The method employed is necessarily a tedious one, as it must consist in the careful comparison of closely related forms.

A. Tanaidae. I have spent some time in working out the Tanaidae of the Bay of Naples and my results are given in detail in the appendix to which the curious reader may be referred.

Within the family of the Tanaidae certain genera stand apart such as *Tanais*, *Alaotanais*, *Anarthrura* and others: but there is a compact group of very closely allied species which do not exhibit

any marked break: this group includes the genera *Leptochelia, Heterotanais, Paratanais* and then the blind genera *Leptognathia, Tanaopsis,* and *Typhlotanais.* This group is held together by the possession of a comb on the chela (Pl. 20, Figs. 7, 21 etc.), by the form of the antennae in the male, and the absence of any other marked differences which split off certain of the other genera. The most perfect series from our point of view goes through the species of *Leptochelia* to *Paratanais, Heterotanais* standing apart through qualitative variations; and the passage from *Paratanais* to the blind genera, though I think certain, is not very immediate. Our method is first to describe the kind of high and low dimorphism that exists within the limits of a large species and then see if our series of allied species fits into any scheme with relation to it. The species chosen is *Leptochelia dubia.* There has been much difficulty with regard to the limits of this species and this is reasonably cleared up in the Appendix. The variation in size of 74 definitively adult males is given in Table 2; it extends from 2—4 mm.; and in the degree of development of the chela, as measured by the length of the forceps, it exhibits the phenomenon of high and low dimorphism very markedly. Figures drawn to scale of chelae of high and low males are given (Figs. 7, 8 and 9). The antennae of the male is long and has from 9—11 joints (Figs. 3 and 4). It must be noticed that low males have often longer and more numerous sensory hairs than high males (Figs. 3, 4, 5 and 6). (The relation of these high and low males to Fritz Müller's males is discussed in the Appendix). All the males have the mouth parts degenerate: up to the last moult they have the form shown in Figure 10. The adult oviferous females have the form shown in Figures 11—13; they measure about 3 mm. The chela is very different to that of the male, being much smaller and lacking the tubercles on the lower limb. The antenna also is quite different, being 3-jointed and destitute of sensory hairs. The uropod of the adults of both sexes has a 6-jointed endopod and a one-jointed exopod. During the larval stages the endopod steadily increases in size proportionately to the exopod, as shown in the series Figs. 14—17. We must now look for a moment more narrowly at the chela of the male. In Fig. 7 which depicts the chela of a high male it should be noted that the two serrated tubercles on the lower arm of the forceps are far apart, but much more nearly approximated in the low male Fig. 8, while in Fig. 9 the two tubercles are running together with a continuous line of serration between

them. Furthermore it should be observed that the comb of the small chela is very large compared to that in the large chela.

We have now to trace our series among the allied species. Firstly there is a form described by DOLLFUS (10), *L. corsica* which measures 5 mm., and he says in relation to the male: "La forme bien plus allongée des chélipèdes chez le mâle paraît cependant un caractère distinctive assez net." So we may conclude that this form besides being large is also high in regard to the chela. This is the only species of *Leptochelia* which is known to be larger than *L. dubia*. Passing to the smaller forms, the nearest is *L. inermis* (Dollfus) which measures 2—6 mm. This species has the chela in the male a good deal reduced, but the two tubercles are recognizable as such on the lower arm of the forceps. Compared to *L. dubia* therefore it is about middle-sized, and we see that it is low in respect to the chela. The uropod of this species has 4 joints in the endopod and one in the exopod; i. e. it is in a state comparable to the developmental stage of the uropod of *L. dubia* figured in Plate 20, Figs. 15 —17. The next species in the series is *L. mercantilis* (see Appendix page 335 and Figs. 18—23). The male measures 1—5 mm., the female being larger 2.75, but the reduction in size of the male is the important point for us. Corresponding to this reduction we see that the cheliped is greatly reduced in size, being assimilated in its proportions to that of the female, while the two tubercles have become completely fused to form a continuous serrated ridge (Fig. 21). The chela comb is largely developed, and the antennae have long sensory hairs (Fig. 20) two characters which we saw beginning in the low males of *L. dubia*. Finally the uropod has the endopod 4-jointed and the exopod one-jointed (Fig. 23). Meantime the female of this species (Fig. 19) has not deviated in the least from the female of *L. dubia*, except that it is a little smaller and has quite constantly only 4 joints in the endopod of the uropod, when adult and oviferous, whereas the female *L. dubia* as constantly has 6 when adult, though in a developmental stage it passes through the 4-jointed condition of the adult in *L. mercantilis*. The exopod of *L. mercantilis* is still one-jointed but increased in size (Fig. 23).

The next species in *L. mergellinae* (Figs. 24—28). It is very closely allied to the foregoing but differs in being still further reduced in size ($\male$ = 9 mm., $\female$ 1.3 mm.), and in correspondence the chela of male and female are closely similar (Figs. 26 and 27), the antenna has very greatly developed sensory hairs (Fig. 24), and the uropod has still further differentiated on the same lines as the preceding species,

having 4 joints in the endopod and 2 in the exopod (Fig. 28). This little form in its size, chelae, antennae and uropod forms a beautiful transition from the genus *Leptochelia* to *Paratanais*. *P. Batei* (Pl. 21, Figs. 40—43), a typical member of the genus, is a little smaller than *L. mergellinae*, and in correspondence the characters under consideration have progressed a little further than in the foregoing. The chela is yet more reduced (Fig. 40), the antennae (Fig. 42) more stumpy and with longer hairs, the uropod has the endopod and exopod both with 2 joints and practically assimilated, except that the endopod is a little longer and stouter (Fig. 43).

We have so got a perfect transition from *L. corsica* through *dubia, inermis, mercantilis, mergellinae,* to *Paratanais*. We have now to pass to the blind genera, *Leptognathia, Tanaopsis, Typhlotanais* (see SARS, Crustacea of Norway, Isopoda). The striking thing about these forms is the great discrepancy in size between the males and females. Thus in *T. laticaudata*, the male measures 1.4 mm. and the female 3.2 mm. and this is also the case with all the species the males of which are known. The male in the form of the chela, the antenna and the uropod betrays a distinct likeness to *Paratanais* (Figs. 44—46), but it is doubtful how nearly allied they are. These blind forms therefore by no means controvert our rule, because the males belong to a distinctly small category and in correspondence we find the chela reduced and the antenna and uropod developed in the way which we have found to be characteristic of the smaller forms.

The rather anomalous species included in the genus *Heterotanais* (Pl. 21, Figs. 29—39) differ qualitatively from the forms considered in several respects, especially in the curious broken form of the chela in the male and the swollen antennae of the female (Figs. 31 and 34). We are here confronted with a qualitative difference which is very hard to deal with and we shall find this also to a certain extent in the Lamellicornia.

We may now tabulate our series as follows, passing from large forms with highly differentiated chelae in the males, with long antennae provided with few and short sensory hairs, with an uropod in which the endopod is much longer than the exopod, to smaller and smaller forms in which these characters become progressively altered in a definite way. These forms are:

L. corsica

L. dubia $\begin{cases} \text{high} \\ \\ \text{low} \end{cases}$ *Heterotanais*

L. inermis

L. mercantilis

L. mergellinae *Leptognathia*

Tanaopsis

Typhlotanais

Paratanais Batei

Now we have seen that within the species *L. dubia*, high and low males occur which differ from one another in two of the characters under consideration, namely the chela and the antenna; while the uropod having its two branches equalized is intelligible on the hypothesis that the smaller species have been split off at a so to speak larval stage in the growth of the larger forms.

The coincidence then of this high and low dimorphism within the species with the existence of high and low species in a compact group appears to me to point to the principle of high and low dimorphism as an important factor in their evolution. For besides their size and the characters which concern the secondary sexual characters and the uropod, the different species of this group are practically indistinguishable. There is one other fact which seems to me to show that these species are to be regarded as races which have been split up partly owing to changes in the stage of growth at which maturity is reached. And this is that the females of the smaller species appear to breed much faster and take less time in becoming mature than the larger forms, and this is the more marked the smaller the species is. Thus one finds more than half the females of *P. Batei* at all times of the year with eggs, but only a small percentage, perhaps $10\,\%$ of *L. dubia*. This appears to me to be of significance.

We must now look for parallel facts in the Lamellicornia.

B. Lamellicornia. It is impossible to maintain that the principle of high and low dimorphism is the sole factor in the evolution of the groups considered; we may go further and say that it is equally impossible to claim that the differentiation of the secondary sexual characters is solely due to this principle. Mr. Arrow, of the British Museum, to whose courtesy I am much indebted, pointed

out to me many peculiar features in the secondary sexual characters
of the Lamellicornia, many of them concerning qualitative differences
in colour and in structure which are quite impossible to bring under
the quantitative rule under discussion. But a general review of the
secondary sexual characters of the Lamellicornia, in so far as they
are quantitatively estimable, affords the most convincing evidence
of the presence of high and low dimorphism as a differentiating
factor. From the mass of material which I have gathered, only a
few most striking instances will be selected for discussion here.
The two genera *Catharsius* and *Copris* belong to the Copridae verae.
The males are distinguished from the females by the presence of
a projecting thoracic ridge and a salient clypeal horn, which are
rudimentary in the female. In *Catharsius* we may start from *C.
molossus* (Textfigs. 10 and 11) a large form with a range of variability
in total length from about 40—22 mm., the high males graduating
into the low and so into the female condition in their secondary
sexual characters. Now as the species of *Catharsius* get smaller and
smaller the sexual differences in the thoracic ridge and the clypeal
horn in the males and females become less and less, until we come

to exceedingly small forms as
C. latifrons, inermis, and *opacus,*
measuring from 15—16 mm. in
which there is no external differ-
ence in the sexes visible. (See
Textfigs. 12 and 13 *C. latifrons*.

Fig. 10.

Fig. 12.   Fig. 13.   Fig. 11.

In the genus *Copris* the larger species have highly marked
sexual differences, and here again we pass in a series to very small
forms as *C. reflexus, minutus* and *laeviceps,* measuring about 11 mm.,
in which the males and females have been entirely assimilated by
the suppression of the secondary sexual characters.

In this way the small species of *Catharsius* and *Copris* come to
converge upon one another in the most remarkable manner, but

this they do only as concerns size and the suppression of the secondary sexual characters, because the structure of the keels on the outer edge of the tibia of the hind leg, a non-sexual character, differs more in the small species of *Catharsius* and *Copris* than in the large.

In these two genera then the development of the secondary sexual characters in the male is a function of the total size, and they afford very good instances of high and low dimorphic species.

The next genus selected is *Euchirus*, a genus of the Melolonthidae. Here a totally different structure is affected by the sexual differentiation, namely the forelegs which in the males are immensely elongated and furnished with antler-like tynes. *E. longimanus* is the largest species known but with a wide range of variation, at any rate from 81 mm. —58 mm. in total length, and the phenomenon of high and low dimorphism is markedly apparent.

From this species we pass by steps to the smaller forms *E. Macleayi* and *E. Parryi*, and so to *Proponaeus* in which the size is steadily reduced, and in correspondence the ratio between the total length and the length of the forelegs becomes also reduced, so that in the last named form, which differs generically in unimportant details from *Euchirus*, the forelegs of the male have very closely approached those of the female in proportions and structure.

In the next two genera selected, *Golofa* and *Dynastes*, members of the Dynastidae, we obtain excellent series, in which the males of the larger species of the genera as respects the thoracic and clypeal horns are high in comparison to the smaller species. In these cases we will give average measurements made up from a series of measurements for each species which included the extreme types as well as the average condition.

In *Golofa* we have:

	Mean body length	Mean ratio	Clypeal horn Body length
G. Porteri	60	0.44	
G. eacus	41	0.27	
G. aegeon	38	0.17	

In *Dynastes*:

	Mean elytron length	Mean ratio	Thoracic horn Elytron length
D. hercules	46	1.4	
D. hyllus	35	0.7	

22*

Now the species within the limits of each genus are very closely allied, being differentiated by constant but detailed differences in marking and structure, and they show this remarkable gradation in the degree of development of the secondary sexual character correlated with the total size.

Sufficient evidence has now been produced to show that several widely separated genera of the Lamellicornia follow the rule which was postulated to meet the supposition that the principle of high and low dimorphism within the limits of a species can be extended to a progressive differentiation in a group of closely allied species. It may be suspected that we have merely selected favourable and suppressed unfavourable evidence. This is not the case; the only instance in which an apparent contradiction to the rule is found is in the genus *Goliathus*, where the smaller species have not suffered a disproportionate decrease in the secondary sexual characters. Nor in the larger species can I find any evidence of the occurrence of high and low dimorphism within the limits of a species, so that even this single instance does not definitely contradict us.

C. Pectinicornia. LACORDAIRE divides the Pectinicornia into Lucanidae and Passalidae, but the Passalidae do not exhibit any high degree of sexual dimorphism, so I have neglected them. The Lucanidae are nearly all highly sexually dimorphic, the characters affected being the mandibles, and to a less extent the head, prothorax and legs. The mandibles of the male are often hugely developed, those of the female being always much smaller; and throughout the whole group the phenomenon of highness and lowness is of quite universal occurrence. That this factor has been an important, if not the most important, factor in the evolution of this group, is I think thoroughly borne out, but except in one or two genera we do not meet with quite such striking series as in the Lamellicornia, because long series of very similar species do not occur. We are also troubled by the great qualitative differences which exist between closely allied species, and even between individuals of the same species. Thus in certain species of the genus *Odontolabis*, e. g. *O. Brookeanus*, I have observed in three similarly sized males three quite different types of mandible. This kind of variation is evidently a kind of high and low polymorphism, but it is not at all strictly coincident with variations in size.

I do not intend going into the same detail with these beetles as with the Lamellicorns, since it would simply mean repeating the

same kind of evidence: but I will indicate which genera chiefly show evidence of our principle. In the genera *Pholidotus*, *Chiasognathus*, *Lamprima*, *Lucanus*, *Odontolabis* and *Cladognathus*, we do not get any long continuous series of species graduating into one another, but with a very high degree of generality it is found that the larger species are much more highly sexually dimorphic than the smaller, and there is no clear instance of the opposite case. In individual cases we get obvious instances of one species being high to a smaller and very closely allied low species.

The genus *Cyclomatus* gives a very perfect series of closely similar forms passing from the large *C. tarandus* where the mandibles may be as long as the body to smaller and smaller forms, until in *C. stryiceps* the highest males have mandibles less than half the body length. The genera *Hemisodorcus*, *Eurytrachelus* and *Dorcus* give similar but not such perfect series.

We have so far mentioned all the genera of Lucanidae without omission: the rest of the genera contain much smaller forms with their secondary sexual differences very much reduced; consequently in the majority of cases, it is hard to detect the presence of our principle. On the whole the Lucanidae afford very definite support and confirmation to the general law which was found to be of application to the Tanaidae and Lamellicornia, in this case the character affected being quite new, namely, the mandibles.

6. Conclusion.

In the foregoing paragraphs it has been shown that the differentiation of the males of many species of Arthropods into high and low forms is of wide occurrence in distantly related groups which show a high degree of sexual differentiation. The high and low dimorphism may be facultative, as in those cases in which the low male by growth passes through an intermediate condition to the high male, or definitive, as in those cases where growth ceases on the assumption of the mature condition. The development of the secondary sexual characters is strictly correlated with that of the primary sexual development, so that the condition of highness and lowness in the secondary sexual characters must stand in relation to some modification in the condition of the primary sexual development, as defined in Section 4.

In the Tanaidae, Lamellicornia and Pectinicornia evidence was produced to show that the differentiation into high and low males within the limits of a species has widely influenced the progressive differentiation among the different closely allied species of many groups.

Now this means that the modifications in the primary and secondary condition of various species which leads to high and low dimorphism within the limits of a species, have operated progressively in the evolution of these forms. There can be little doubt that these modifications are primarily induced by the conditions of life, especially of nutrition, acting upon the sexual organization of the male. For we know that the sexual organization is largely influenced by particular conditions of life, by nutrition and most strikingly by the presence of particular parasites, as is evinced in the phenomenon of Parasitic Castration. And it is well known to breeders of insects that the size to which the adult attains can be very greatly influenced by the amount and quality of nutrition supplied to the larva.

Now if we assume, as I believe we must, that the phenomenon of high and low dimorphism is an effect largely produced by the influence of external conditions on the sexual organization, it appears that this influence has operated continuously in specific differentiation, in other words that these influences have become inherited in some manner. But before dismissing this hypothesis as assuming the inheritance of acquired characters, we must reflect with what we are dealing. We are dealing with characters that do not primarily belong to the body, but to the reproductive organization. It is the reproductive organization that is affected in the phenomenon of high and low dimorphism, and so there is here not the same a priori difficulty in the transmission of such affections, as exists in cases where the body only is influenced. We are however in need of some material theory by which the modifications induced in the reproductive system can be transmitted through the germ cells to succeeding generations. A material theory of this nature is, I believe, afforded by a series of facts and experimental results, which I hope to describe in a future work, but to which I cannot further advert here.

Appendix 1. The Tanaidae of the Bay of Naples.

With descriptions of new species.

Leptochelia (Pl. 20, Figs. 1—17).

L. dubia = *L. dubia* (Kröyer) = *Algicola* (Harger & Dollfus) + *Savignyi* (Kröyer & Sars) + *neapolitana* (Sars).

Remarks. Since the species has received many names and has often been described and figured it is only necessary for me to give my reasons for believing that all the forms described under the various names given above are really only one species.

The female of this species was first described as *Tanais Savignyi* by Kröyer from Brazil (Nat. Tidskr. 4. Bd. p. 168 Tab. 2 Figs. 1—12) and the male as *T. Edwardsii*, but Dana had previously (1849, U. S. Expl. Exped. Crust. Vol. 2) suggested the generic name *Leptochelia* for *L. minuta*, an allied form. Kröyer also described what he considered another species as *T. dubius* from a single Brazilian specimen (loc. cit.), but this from his figure was evidently an immature specimen, because it had only 5 joints in the endopod of the uropod. It may therefor be ignored. Subsequently Bate & Westwood (British Sessile-eyed Crustacea) described *L. Savignyi* as *L. Edwardsii*; Harger (Report on Marine Isopoda of New-England) has described it as *Algicola*, and finally Sars in his work (Middelhavets Saxisopoda) made three species out of it, *L. Savignyi*, *dubia* and *neapolitana*. Professor Sars, courteously replying to my enquiries, admits that the examination of a larger material than was at his disposal may break down the distinction between his three forms. After examining several thousand female specimens and about 80 males my conclusion is that these three forms constitute one species which in future should be known as *L. dubia*.

The form described by Sars as *L. Savignyi* ♀ (our Fig. 10) is in reality an immature male of *L. dubia*, which passes through this stout form with 4-jointed antennae and rather powerful chelae before assuming the adult male state. Although females do occur (Fig. 13) occasionally with 4 joints in the antenna, these females do not have the stout body and chela characteristic of the *Savignyi* form. The typical *Savignyi* form, if examined by sections, are found to possess testes, and never ovaries, while it is possible, fairly

frequently, to see a *Savignyi* form with the antenna of the adult male telescoped up in the 4-jointed antenna of the younger stage.

The separate species made by SARS and others for *L. Savignyi* therefore entirely break down, this form proving to be an immature male of *dubia*. The distinction between the females *dubia* and *neapolitana* does not hold at all if a large series be examined.

Turning to the males SARS attempts to make distinctions on the number of joints in the antennae. Our 74 males in this respect graduate into one another quite perfectly, and in respect of every other character examined it was found quite impossible to split them up into more than one species.

The total number of joints in the antennae of our males were as follows:

No. of joints	9	10	11	12
Frequency	16	37	18	1

and 2 specimens had 9 joints in one antenna and 10 in the other.

Now SARS' 3 kinds of male are separated as follows:

L. Savignyi ♂	9 joints in whole antenna
L. dubia ♂	12 joints
L. neapolitana ♂	8 joints.

There is another point to be discussed. FRITZ MÜLLER in his Für DARWIN describes a very pronounced form of dimorphism among the males of a species of Tanaid which he calls *T. dubius* (?) (KRÖYER). The figure which MÜLLER gives leaves no doubt that he was dealing with our form *L. dubia*, or at any rate with a very closely allied species. He states that the males of this form in Brazil occur under two quite different forms, the one with highly differentiated chelae and short sensory hairs on the antennae, the other with femalelike chelae and antennae with long and numerous sensory hairs.

Since MÜLLER, no one has seen the second of these forms. DOHRN (9) suggested that a small male which he found in company with *L. dubia* and to which he could supply no female might be this form, but this male has turned out to be *Heterotanais anomalus* (Sars) to which I have discovered the female (see below). Now with regard to FRITZ MÜLLER's statement it is true that the males of *L. dubia* exhibit a kind of dimorphism which we have described in some detail on pp. 319 and 324, and this dimorphism approaches

the condition described by Müller, but is never so marked nor is it discontinuous, the types graduating into one another. We must therefore admit for the present that although the kind of dimorphism described by Müller does not occur in the Mediterranean L. dubia, there is a possibility that the Brazilian species has progressed further on the same lines and that the two forms of male described by Müller really do belong to one species. On the other hand the forms discovered by me and to be now described, namely L. mercantilis and mergellinae and also Dollfus' form L. inermis, correspond very well with Müller's low male, and since these species may be found mixed up with L. dubia, and their females are only distinguishable from L. dubia ♀ by the less number of joints in the uropod, it is quite possible that Müller has mixed up two species. It appears to me that the only way this matter can be settled is by examining the Brazilian species. Stebbing's suggestion that the low male of Müller was in reality an immature form is I think wrong; the immature male of L. dubia is the form which has been described as L. Savignyi: and there is no evidence of the existence of a form intermediate between this and the adult male. L. dubia occurs at Naples all round the shore and at moderate depths, especially among the coralline algae.

L. mercantilis. — New species. — Pl. 20, Figs. 18—23.

Male. Length 1.5 mm., Breadth 0,25 mm. Mouth parts completely degenerate as in L. dubia. 1st antenna has 7 joints, sense-hairs not very numerous, about 4 to each joint of flagellum, but slightly longer than in L. dubia. Eyes poorly developed. Chelae not more strongly developed in male than female; biting edge of carpopodite continuously serrated; comb has 14 bristles. Uropod has endopod with 4 joints; exopod with 1 joint, longer than in L. dubia.

Female. Length 2.75. Very hard to distinguish from L. dubia ♀, the only constant distinguishing features being (1) the endopod of uropod has 4 joints, exopod being one jointed but conspicuous: (2) 1st antenna which is 3-jointed has middle joint always tinged with purple.

This species occurs in fair abundance in the Porto mercantile and militare among the polyzoan *Bugula purpurotincta* on which it feeds, the whole body containing oil drops whose colour is plainly derived from the Polyzoan. In this material no other Tanaid occurs, but where the Polyzoan is mixed with coralline alga, L. dubia may

be mixed with *L. mercantilis*. There can be no doubt however that the two are quite distinct though very closely allied species.

L. mergellinae. — New species. — Pl. 20, Figs. 24—28.

Male. Length 0.9 mm. Mouth parts degenerate as in preceding. 1ˢᵗ antenna has 8 joints. the proximal joints of flagellum being rather swollen: sensory hairs numerous and long. Eyes well developed. Chelae very similar to those of *L. mercantilis* in every particular; comb has 11 bristles. Claws on walking legs very long. Uropod has endopod of 4 joints, exopod of 2.

Female. Readily distinguishable from females of *L. dubia* and *mercantilis* by their small size and uropod, which has a 4-jointed endopod and 2-jointed exopod.

This species occurs in no great abundance at Posillipo and Mergellina in rather muddy material consisting chiefly of the roots of *Posidonia Carolinii*. It affords a very beautiful transition to *Paratanais Batei*.

Heterotanais.

H. anomalus (Sars) ♀ nov. (Pl. 21, Figs. 29—35).

Male. Described by Sars (Middelhavets Saxisopoda). Chela brush has 11 bristles.

Female. 1.5 mm. long. At once distinguished from young *Leptochelia* by the short and very stout 1ˢᵗ antenna, the presence of two joints in the exopod of the uropod and 4 joints in the endopod. The joint of the cheliped which precedes the chela has an overlapping lobe.

Dohrn [9] discovered the male of this species, and as it occurred mixed with *L. dubia* and there appeared to be no female corresponding to it. he suggested that it was Müller's low male of *L. dubia*. Sars found the male again but though he did not discover the female, he believed on general grounds that it belonged to a separate species. Dohrn's suggestion must now be finally given up as I have found the oviferous female corresponding to the male, and also the male and female of a similar closely allied species. *H. anomalus* occurs in very small numbers mixed up with *L. dubia*.

H. magnus. — New species. — Pl. 21, Figs. 36—39.

Male. Length 2.5 mm. Very similar to *H. anomalus* save in size. but first antenna has more joints, viz. 13 as against 10, and the chela is more strongly developed, with 17 bristles in comb.

Female. Length 3 mm. Resembles in all particulars *H. anomalus* but is far more strongly built and the 1st antennae are even more swollen.

This species is separated from *H. anomalus* because it never occurs mixed up with it and inhabits a totally different station. viz. the deeper water and muddy material of Posillipo and Mergellina. Otherwise I should call it a "high" variety of *H. anomalus*.

I now append a list of the species of Tanaidae found by me in the bay.

Tanais vittatus ♂ and ♀ rare. All stations.

T. Carolinii ♂ and ♀ rare. All stations.

Paratanais Batei ♂ and ♀. 2-3 meters in *Amphioxus* sand.

Tanaopsis laticaudata ♂ and ♀. Deep muddy material. Mergellina.

Leptognathia brevimana ♂ and ♀. Same material as above.

Pseudotanais mediterraneus. Only ♀. Same material.

Leptochelia corsica. Only ♀. Coralline algae on Posillipo shore.

L. dubia ♂ and ♀. Very abundant in coralline algae at Santa Lucia.

L. mercantilis ♂ and ♀. In *Bugula purpurotincta* at Porto militare and mercantile.

L. mergellinae ♂ and ♀. At Mergellina, deepish water.

Heterotanais anomalus ♂ and ♀. With *L. dubia*.

H. magnus ♂ and ♀. Mergellina and Posillipo.

Appendix 2.

Table 1.   Correlation of chela breadth and thoracic length, *I. scorpio* ♂.

Chela breadth in mm.

	1	2	3	4	5	6	7	8	9	10	11	12	
9	2												2
10	S	3	1										12
11	1	1S	3										22
12		23	22										45
13		12	39	10									61
14		4	20	24	1								49
15		2	3	26	7								3S
16		5	11	4	6	4							30
17			15	4	6	2							27
1S			10	7		2	4						23
19			5	9		2	6	3					25
20			2	6	1		2	12					23
21						1	1	17	12	4			35
22							3	25	13	1			42
23								7	14	3			24
24								2	12	S	1		23
25									2	5	3		10
26										1	1	3	5
	11	67	131	90	21	11	13	35	46	46	1S	7	496

Carapace length in mm.

Table 2. Correlation of chela length and body length, L. dubia ♂.

Scale of chela length in mm.

Scale of body length in mm.	0.1	0.2	0.3	0.4	0.5	0.6	0.7		
2	6	18	4	1				29	2
2.5		5	12	8	2			27	2.5
3				3	8	3		14	3
3.5					1		2	3	3.5
4							1	1	4
	6	23	16	12	11	3	3	74	
	0.1	0.2	0.3	0.4	0.5	0.6	0.7		

List of Literature.

A. Referring to high and low dimorphism.

1. **F. Müller**, Facts for Darwin. Chap. 4. London 1869.
2. **W. Bateson & H. H. Brindley**, On some cases of variation in secondary sexual characters. in: Proc. Z. Soc. London f. 1892, 1893 pag. 585.
3. **A. Giard**, Dédoublement des courbes de Galton. in: C. R. Soc. Biol. Paris (10) Tome 1 1894.
4. **J. Th. Oudemans**, Falter aus castrirten Raupen. in: Z. Jahrb. Abth. Syst. 12. Bd. 1898 pag. 71.
5. **V. L. Kellogg**, Influence of the Primary Reproduction Organs. in: Journ. Exper. Z. Baltimore Vol. 1 1905 p. 601.
6. **G. Smith**, Metamorphosis and Life history of *Gnathia maxillaris*. in: Mitth. Z. Stat. Neapel 16. Bd. 1904 pag. 469.

B. Referring to Tanaidae.

7. **H. Kröyer**, Nye Arter af Slägten *Tanais*. in: Nat. Tidskr. 4. Bd. 1842 pag. 167.
8. **G. O. Sars**, Revision af Gruppen: Isopoda chelifera. in: Arch. Math. Naturv. 7. Bd. 1881.
—— Nye Bidrag til Kundskaben om Middelhavets Invertebratfauna. 3. ibid. 11. Bd. 1886 pag. 263.
—— Crustacea of Norway. 2. Isopoda. 1899.
9. **A. Dohrn**, Untersuchungen über Bau und Entwicklung der Arthropoden 2. Heft. Leipzig 1870 pag. 129.
10. **A. M. Norman**, British Isopoda chelifera. in: Ann. Mag. N. H. (7) Vol. 3. 1899 pag. 317.
11. **A. Dollfus**, Campagnes de la Melita. Tanaidae récoltés par M. Ed. Chevreux [etc.]. in: Mém. Soc. Z. France Tome 11 1898 pag. 35.

Explanation of Figures.

The magnifications are only given approximately. Figures 7, 8, 9, 21, 22, 26, 28, 38, 40, 41, 44, 45 representing chelae are all drawn to the same scale.

Plate 20.

Figures 1—17 refer to *Leptochelia dubia*.

Fig. 1.   High male. × 22.

Fig. 2.   Low male. × 22.

Fig. 3.   1st antenna of high male. × 50.

Fig. 4.   1st antenna of low male. × 50.

Fig. 5.   First 3 joints of 1st antenna, high male. × 125.

Fig. 6.   First 3 joints of 1st antenna, low male. × 125.

Fig. 7.   Chelae of high male. × 125.

Fig. 8, 9. Chelae of low males. × 125.

Fig. 10. Male, before last ecdysis. × 54.

Figs. 11—13. Females, different types. × 54.

Fig. 14. Uropod of larva taken from brood pouch. × 125.

Figs. 15—17. Stages in developement of uropod. × 125.

Figures 18—23 refer to *L. mercantilis*.

Fig. 18.   Male. × 22.

Fig. 19.   Female. × 22.

Fig. 20.   1st antenna of male. × 125.

Fig. 21.   Chela of male. × 125.

Fig. 22.   Chela of female. × 125.

Fig. 23.   Uropod. × 125.

Figures 24—28 refer to *L. mergellinae*.

Fig. 24.   Male. × 70.

Fig. 25.   Female. × 70.

Fig. 26.   Chela of male. × 125.

Fig. 27.   Chela of female. × 125.

Fig. 28.   Uropod. × 125.

Plate 21.

Figures 29—35 refer to *Heterotanais anomalus*.

Fig. 29.   Male. × 54.

Fig. 30.   Female. × 54.

Fig. 31.   Chela of male. × 100.

Fig. 32.   Chela of female. × 100.

Fig. 33.   1st antenna of male. × 100.

Fig. 34.   1st antenne of female. × 100.

Fig. 35.   Uropod. × 100.

Figures 36—39 refer to *H. magnus*.

Fig. 36.   Male. × 40.

Fig. 37.   Female. × 40.

Fig. 38.   Chela of male. × 125.

Fig. 39.   Uropod. × 125.

Figures 40—43 refer to *Paratanais Batei*.

Fig. 40.   Chela of male. × 125.

Fig. 41.   Chela of female. × 125.

Fig. 42.   1st antenna of male. × 125.

Fig. 43.   Uropod. × 125.

Figures 44—46 refer to *Tanaopsis laticauda*.

Fig. 44.   Chela of male. × 125.

Fig. 45.   Chela of female. × 125.

Fig. 46.   Antenna of male. × 125.